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Sudden collapse of xylophilous bee populations in the mountains of northern Utah (USA): An historical illustration

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Abstract

A scarcity of studies of the dynamics of wild bee populations hampers conservation efforts by bee ecologists and conservationists. Present limited information suggests that bee populations are highly unpredictable from year-to-year. Here we present an historical data set from nine sites replicated in 1984 and 1985 that demonstrates extreme between-year variability in numbers for 19 xylophilous bee species. Sixteen of those species produced far fewer nests in 1985, and 13 species in 1985 produced less than a third the number of nests produced in 1984. We argue that the 1985 collapse was not due to semivoltinism, i.e., the absence of morphs that require two years to mature, or to excessive sampling in 1984, but to a record cold period from January to March 1985 which likely killed most diapausing bees. Such events illustrate the dynamism of wild bee populations and thereby the large number of years needed to establish statistically significant population trends. We suggest that the current emphasis by bee conservationists to promote widespread surveillance monitoring programs is misguided and that funds are more effectively spent on hypothesis-driven targeted monitoring and on actions to actually reclaim degraded wild bee habitat.

Key Words

Anthophila, Megachilidae, weather, parsivoltinism

Introduction

Insect population numbers, including those of wild, native bees, are notoriously variable from year-to-year (Hanski 1991). In early reviews, Roubik (2001) and Williams et al. (2001) found that bee populations were highly dynamic and subsequent studies have generally confirmed that finding. For example, Roubik and Villanueva-Guttierrez (2009) reported great variation in nesting by bees utilizing trap-nests over a 17-year period. Franzen and Nilsson (2013) followed twelve populations of a rare bee in Sweden over nine years and found that only one population persisted through the entire period. Ogilvie et al. (2017) found that numbers of three species of bumblebees visiting flowers in subalpine Colorado meadows varied greatly over eight years. Graham et al. (2021) reported significant declines and recoveries of several blueberry-visiting native bee species over a fifteen-year period. A recent study of common orchid bees in Panama by Roubik et al. (2021) reported much inter-annual variation in population numbers of common species but detected no significant trend over the entire 40-year period. Other studies of differing durations have all reported great year-to-year changes in species composition and abundance, and in host-plant associations in bee communities (Tepedino and Stanton 1981; Alarcon et al. 2008; Herrera 2019).

Despite the cautions of Roubik (2001) and Williams et al. (2001) that detecting significant trends in bee species population size over time may be a formidable task, and findings of wide swings in bee population numbers over periods of time longer than a few years, calls persist for an intensive continent-wide program in North America to monitor native bee species population sizes, and bee

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species richness and diversity (e.g., LeBuhn et al. 2013; Woodard et al. 2020). This is, in part, due to the importance of bees to crop and wild plant pollination (Klein et al. 2007; Ollerton et al. 2011) and to the burgeoning number of reports of bee declines (e.g., Powney et al. 2019; Duchenne et al. 2020; Zattara and Aizen 2021). Concern over bee declines has also sparked calls for publication of older, standardized, data sets which might expand our understanding of the behavior of bee populations (Wagner et al. 2021).

In that spirit, we present an older, brief data set, an extension of a previous paper in which we described cohort-splitting and parsivoltinism in several xylophilous species of *Osmia* bees (Tepedino et al. 2022). Progeny of parsivoltine species develop to the adult stage in either one or two years and sibs of both year-morphs are commonly found in the same nest (Torchio and Tepedino 1982). Relevant to interpreting our present report is the earlier finding that the incidence of two-year morphs increases with altitude and lower average temperatures (Tepedino et al. 2022).

We first provide an example of extreme temporal and spatial dynamism in northern Utah populations of several solitary bee species and then speculate on the possible causes of such a phenomenon and what it signals for surveillance monitoring efforts for species of wild bees.

Methods

Our study was conducted in Logan Canyon, in northern Utah (Cache, Rich Cos., Wasatch-Cache National Forest), United States of America in 1984 and 1985. Logan Canyon rises from about 1300 m to 2500 m in a northeasterly direction through the Bear River Range of the Wasatch Mountains. Site elevations and geographic locations are shown in Table 3; a map can be found in Tepedino et al. (2022).

Females of target species readily nest in tunnels drilled in artificial wooden domiciles (pine trap-blocks). Sampling with trap-blocks avoids the need for precise synchronization with bee flight seasons so important when other methods (e.g., bowl-traps) are used because blocks are in place for the entire season. Populations were sampled at nine sites, beginning in April 1984 and again in 1985. Sites were selected along an elevation gradient in the mountain brush zone (Banner 1992) of open shrub (e.g., *Artemisia*, *Quercus*, *Cercocarpus*, *Acer*)/grassland habitats with diverse, mostly perennial, wildflowers in the Asteraceae, Plantaginaceae, Fabaceae and other families. Block placement closely followed snow melt; thus, blocks at lower southwestern sites were positioned earlier than blocks at higher northeastern sites.

Sites and methods in the two years were identical. At each site, ten nest blocks were placed 4–8 m apart in unshaded spots. Blocks were attached with screws and bolts to the top of meter-high posts and faced east to capture the morning sun. Each block contained 50 drilled holes arranged in five columns and ten repeating rows. Each row contained an unvarying sequence of drilled hole sizes: 2, 4, 6, 8, 10 mm.

Blocks were collected after several mid-October frosts when bee activity and flowering had ceased, and stored in an unheated garage in Logan, Utah. Nest dissection, description and preliminary identification commenced immediately and proceeded for several weeks. The contents of each nest cell were recorded and placed in gelatin capsules which were attached to two-sided adhesive paper on thick cardboard (sticky boards) and returned to the garage. After all nests were dissected, all sticky boards were moved to a temperature-controlled room at 3–5 ºC for the normal winter dormancy period.

In April of the year following collection, sticky boards were removed from the temperature room, held for a few days at room temperature (~18–20 ºC) and then placed in incubators at 29º C to accelerate emergence. Boards were checked for emergence of adult bees twice daily. Upon emergence, adults were frozen, pinned, labelled, identified and associated with their natal nests. Identifications were made by the junior author by comparison with specimens in the National Bee Collection at the United States Department of Agriculture, Agricultural Research Service Pollinating Insect Research Unit in Logan Utah and confirmed or corrected by Terry L. Griswold, Curator of the collection where voucher specimens are deposited.

Nests from all sites were combined within years for each species and comparisons of numbers of nests were made between years with the Wilcoxon Signed Rank Test, a non-parametric version of the paired t-test (Zar 1999). Temperature records, mean monthly minimums and daily minimums, were retrieved from pertinent National Oceanic and Atmospheric Administration weather stations in the Bear River drainage (www.ncdc.noaa.gov) Table 3.

Results

We recorded 19 species of bees that produced at least 10 nests in our trap-nests in either 1984 or 1985 (Table 1). No species was recorded only in 1985.

Of the 19 species that produced at least 10 nests in either 1984 or 1985 (Table 1), 16 produced fewer nests in 1985. Of those, 15 species at least halved their 1984 output in 1985; in 1985, 13 species produced less than a third the number of nests produced in 1984 (Table 1). A comparison, between years, of nests produced by species was highly significant (Wilcoxon Signed Rank Test, $P<0.001$).

Based on our earlier finding of significant differences in voltinism between high and low elevation populations (Tepedino et al. 2022), we grouped sites by elevation (below or above 1850 m) and compared the number of nests constructed by species between years (Table 2). Again, we found highly significant differences with approximately six times as many nests being produced in 1984 as in 1985 for both elevation groups (both <0.01).

Table 1. The number of nests made by 19 species of xylophilous bees at each of nine sites in 1984/1985. Only species with >10 total nests shown. [1] = Low elevation sites. All Latitudes are decimal 41, all Longitudes are decimal -111; [2] = parsivoltine species. Emboldened species (3) built more nests in 1985 than in 1984.

Sites	LC3[1]	LC4[1]	LC5[1]	LC6	LC7	LC8	LC9	LC10	BL[1]	TOT
El (m)	1605	1553	1848	2074	2134	2280	2378	2436	1794	
Lat	.7475	.7608	.8335	.9387	.9628	.9593	.9413	.9255	.8781	
Long	.7436	.7075	.5955	.5558	.5306	.5079	.4812	.4713	.3660	
Species										
***Ashmeadiella bucconis* (Say, 1837)**	12/10	0/3	0/1	0/0	0/0	0/0	0/0	0/0	0/0	12/14
Chelostoma minutum Crawford, 1916	4/2	23/14	0/0	0/0	0/1	0/1	0/0	0/0	0/0	27/18
***Dianthidium ulkei* (Cresson, 1878)**	10/23	0/5	0/0	0/0	0/0	0/0	0/0	0/0	0/0	10/28
Heriades carinata Cresson, 1864	29/0	31/4	1/0	4/1	0/2	0/0	0/0	0/0	0/0	65/7
Hoplitis albifrons (Kirby, 1837)	0/0	0/0	0/0	1/0	0/1	26/3	0/0	3/0	0/0	30/4
Hoplitis fulgida (Cresson, 1864)	0/0	0/0	15/0	20/3	0/0	18/1	4/0	6/0	0/0	63/4
Megachile pugnata Say, 1837	0/0	20/0	35/8	4/3	4/0	0/0	0/0	0/0	0/0	63/11
Megachile relativa Cresson, 1878	1/2	2/1	3/3	18/1	4/6	15/4	4/2	6/1	0/0	53/20
Megachile rotundata (Fabricius, 1787)	38/0	22/9	3/0	0/0	0/0	0/0	0/0	0/0	0/0	63/9
Osmia atrocyanea Cockerell, 1897	0/0	8/0	11/0	0/0	0/0	0/0	0/0	0/0	0/0	19/0
Osmia bruneri Cockerell, 1897	25/9	82/36	242/0	0/0	0/0	17/0	0/1	0/0	238/29	604/75
Osmia californica[2] Cresson, 1864	9/0	6/3	3/0	26/0	0/0	0/0	0/0	0/0	0/0	44/3
Osmia coloradensis[2] Cresson, 1878	20/0	10/0	46/1	40/0	17/3	99/18	26/0	59/0	81/0	398/22
Osmia iridis Cockerell & Titus, 1902	0/0	0/0	13/0	0/1	0/0	0/0	0/0	0/0	0/0	13/1
Osmia kinkaidii Cockerell, 1897	0/0	19/1	4/0	7/5	0/0	20/4	0/0	0/4	25/8	75/22
***Osmia lignaria* Say, 1837**	0/1	1/34	0/0	1/0	0/0	0/0	0/0	0/0	7/0	9/35
Osmia melanopleura Cockerell, 1916	0/0	8/0	5/0	0/0	0/0	6/5	0/0	0/4	0/0	19/9
Osmia montana[2] Cresson, 1864	21/0	4/0	9/0	7/0	0/0	10/2	0/0	9/0	5/0	65/2
Osmia texana[2] Cresson, 1872	42/0	67/1	0/0	0/0	0/0	0/0	0/0	0/0	0/0	109/1

Discussion

Our results illustrate how dynamic populations of native bee species can be from year-to-year and site-to site and are consistent with other reports of inter-annual variation in bee numbers (e.g., Roubik 2001; Williams et al. 2001; Franzen and Nilsson 2013; Graham et al. 2021; Roubik et al. 2021). For example, we found the number of *O. bruneri* nests to vary eightfold across two years and tenfold among sites that differed in 300 m elevation (Table 1); and, that in 1985, the several parsivoltine *Osmia* species recurred at only 27.3% of 1984 sites. Unfortunately, we have no subsequent data to describe how rapidly these populations might have recovered. Data from an earlier unpublished study of several species of xylophilous bees and wasps over seven years in Logan Canyon (1973–1979) also show great inter-annual variation in number of nests though not as exaggerated as that reported here (there were no sudden disappearances of abundant species between years; F.D. Parker, V.J. Tepedino and S. Droege, unpublished). Those data suggest recovery within 5–7 years of species whose populations had greatly diminished in one year. However, those recoveries occurred in the absence of an extreme winter such as was experienced in January-to-March, 1985 (see below).

There are at least three explanations for the observed decline in population numbers in 1985: parsivoltinism, excessive trapping of bees in 1984, and weather. The prevalence of two-year forms in nests from 1984, particularly at elevations above 1850 m, might explain the virtual absence of those parsivoltine *Osmia* species in 1985. However, the decline in numbers of nests occurred not only at upper elevation sites where two-year morphs were predominant but also at lower elevation sites where there were far fewer two-year individuals in 1984 (Tepedino et al. 2022). Indeed, there was no difference between upper and lower sites in the rate of decline in numbers of nests in 1985, suggesting that the decrease in nest numbers was due to something other than parsivoltinism.

A second explanation is that the trapping program of 1984 removed almost all xylophilous bees and greatly depressed reproduction in 1985. What little information is available on the effect of bee removal on subsequent population size does not support this explanation. Only Gezon et al. (2015) have directly tested the effect of removing bees on population numbers in subsequent years. Sampling over four years with pan-traps and by netting they found no change in bee abundance or

Table 2. Mean and median number of nests made by N number of bee species at nine study sites in Logan Canyon in 1984 and 1985. Totals combines data for all sites (19 species) in each respective year. See Table 1 for site designation as lower elevation (LE) or upper elevation (UE).

	Totals		Lower Elevation		Upper Elevation	
	1984	1985	1984	1985	1984	1985
N	19		18		14	
Mean	91.6	15.0	66.3	10.9	25.3	4.1
Median	53.0	9.0	19.0	4.0	6.0	2.0

diversity despite removing over 2800 bees per year. The unpublished study cited above of nine xylophilous bee species in northern Utah over seven years (1973–1979) by Parker, Tepedino and Droege found a significant increase in the nests of one species, a significant decrease in nesting of another species, and no discernable change in seven species. Torchio and Tepedino (1982), also sampling for two years with trap nests in northern Utah mountains, found an increase in nests in the second year for one species (*O. californica*) and a decrease in nests in the other (*O. montana*). We tentatively conclude that sampling such as employed here does not usually depress bee population numbers in the short term though the effect of persistent long-term sampling is unclear.

A more likely cause of the 1985 decline is extreme cold weather which has long been implicated in sudden declines of insect populations (e.g., Ehrlich et al. 1972; Solbreck 1991; Stahl et al. 2006; Graham et al. 2021). The January-to-March period of 1985 had many days of record-breaking cold temperatures at several available weather stations in and near Logan Canyon (Table 3). For example, at each of six weather stations in northern Utah, in the first three months of 1985 there were an average of 50 days that were > 10 degrees colder than the 30-year (1981–2010) minimum average for each of those sites. Indeed, on Feb. 1, 1985, the second coldest temperature ever recorded in the contiguous 48 states, - 56.3ºC, was recorded at Peter Sinks, a natural limestone sinkhole in Logan Canyon (weather.gladstonefamily.net/site/PSINK; elev. 2488 m; Lat 41.9130, Lon -111.5142). Peter Sinks is < 6 km distant from LC6 through LC10 (calculations using Google Earth). Such temperature extremes can have profound demographic and genetic effects on native insect populations (see Filazzola et al. 2021 for a recent review) particularly those that nest aboveground and are unprotected by deep snow. Thus, it is more likely that the much lower temperatures of early 1985 sustained for extended periods decimated overwintering populations of xylophilous bees.

Although our data set spans but two years, and documents an extreme event, the large between-year differences in population numbers warn of the difficulty of uncovering significant population trends for bees by using surveillance monitoring even when several decades of data are available (Tepedino and Portman 2021). In general, the usefulness of surveillance monitoring studies for determining population trends in a timely manner has also been recently questioned by others (Fox et al. 2019; White 2019). Fox et al. (2019), for example, analyzed long-term surveillance data for butterflies and moths of the United Kingdom and concluded that the 10-year trend rule advocated by the International Union for the Conservation of Nature (IUCN) was unreliable because it was "unacceptably biased by the start year." Thomson (2019) reported that a trend of significant declines in pollination services to *Erythronium grandiflorum* over a 17-year period disappeared when nine additional years of data was gathered. Thus, very long monitoring periods are necessary to uncover trends, though whether they yield any actionable information is debatable (Roubik et al. 2021). Others (Powney et al. 2019; LeCroy et al. 2020) used long periods (15 and 33 years, respectively) to report significant declines of bee populations without suggesting actionable remedies to address those declines. When remedies to long-term declines are suggested, e.g., Duchenne et al. 2020, they are non-specific to species and are of a sort that would be recommended without any monitoring at all, e.g., restore degraded habitat.

Bee conservationists are presently caught between the undeniable need for some long-term monitoring studies to learn of the state of pollinator populations, particularly in more pristine locations, and the urgency to restore, at least partially, habitats that have already been degraded. Because funds for conservation of wild bees are limited (Tepedino and Portman 2021), a compromise between short- and long-term efforts should be sought. Rather than the current emphasis on a plethora of scattershot, easily implemented, "monitoring" efforts (Portman et al. 2020), a limited number of well-chosen pristine sites should be selected to serve as long-term monitoring sites (Tepedino and Portman 2021). Concurrently, because bee declines are known to be occurring (Powney et al. 2019; Duchenne et al. 2020; Zattara and Aizen 2021), there is much we can and should do to ease the present plight of wild bee populations (e.g., Potts et al. 2016; Kremen and Merenlander 2018; Forister et al. 2019). The emphasis on surveillance monitoring should give way to targeted-monitoring studies (Nichols and Williams 2006) whose primary objective is testing hypotheses that will lead to management-oriented conservation (Tepedino and Portman 2021).

Table 3. Weather data from 6 NOAA stations (USC# = identification number) in or adjacent to Logan Canyon. Coldest is the coldest day in the month; Mm is the mean minimum temperature for the month (NOAA average 1981–2010); # below >10 Mm is the number of days the minimum temperature was colder than 10 degrees below Mm; the total number of days for the period was 90 (31 for each of January and March, 28 for February). *= Lon -112.

NOAA ID		Lat	Lon	El (m)	Coldest (˚C) /# below >10 Mm			Tot # days below	
Site	USC#		(-111)		Jan	Feb	Mar	Mm	>10 Mm
Cutler	00421918	41.8331	0579*	1308	-15/17	-22/16	6/17	77	50
Hardware	00423671	41.6000	5667	1695	-34.4/15	-36.1/16	-23.9/12	70	43
Laketown	00424856	41.8250	3208	1823	-32.8/18	-36.7/18	-23.3/18	77	54
Lifton	00105275	42.1230	3133	1809	-38.3/19	-40.6/19	-26.7/22	80	60
Richmond	00427271	41.9063	8100	1426	-29.4/19	-32.8/16	-15.6/16	78	51
USU	00425186	41.7460	8030	1460	-22.8/17	-28.3/12	-14.4/12	79	41

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